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TREE RINGS AND KAIBAB NORTH DEER HUNTING SUCCESS, 1925 - 1975[1]

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INTRODUCTION. — Knowledge of the biotic and abiotic factors producing long and short-term changes in numbers provides the basis for managing wildlife populations. Frequently, evaluation of these factors over a long time period is impossible. The large, well-documented past fluctuations of mule deer *(Odocoileus hemionus)* numbers on Arizona's North Kaibab plateau (Rasmussen, 1941; Russo, 1964; Caughley, 1970; Burk, 1973) make it potentially useful for examining long-term effects.

Standardized tree ring widths measure the integrated effects of annual variation in temperature and availability of moisture, and serve as accurate indices of past climatic patterns (Fritts, 1965; Fritts, 1974; Fritts, 1976). Tree ring data are especially applicable in studies requiring long-term data on regional climatic variation (Spencer, 1958; Stockton and Fritts, 1973; Blasing and Fritts, 1975; Nash et al. 1975; Clark et al., 1975). In the present study, growth ring data from woody plants on the North Kaibab were compared with deer hunting success, a frequently used index of animal numbers (e.g. Dasmann and Dasmann, 1963; Smith and Gallizioli, 1965).

Hypothetically, climatic change and its consequent effect on range quality cause changes in deer numbers, perhaps through density-dependent factors related to resource availability (Figure 1). Tree ring widths, range quality, and deer numbers respond directly to climatic variation. Climatic indirectly effects deer numbers through its effect on forage availability (range quality). In this scheme, range quality and deer numbers should correlate positively with tree ring widths.

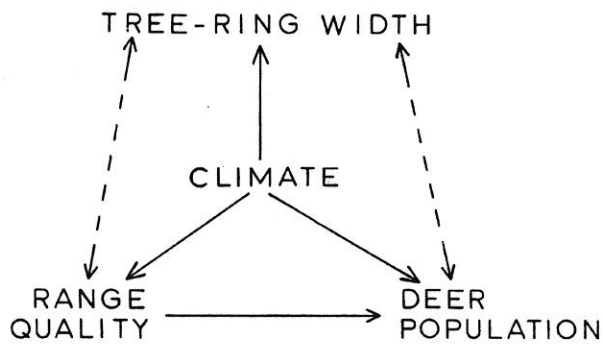

Figure 1. Proposed relationships between climate, tree ring width, range quality, and deer numbers. Solid single-headed arrows represent causal connections between variables; broken double-headed arrows represent correlations.

MATERIALS AND METHODS. — *Study sites.* Two tree ring sampling sites from quite different communities were selected on the Kaibab plateau. One site is in boreal coniferous forest on the upper plateau, 9.7 km east of Highway 67 on Saddle Mountain Road. Abundant tree species are two spruces (*Picea engelmanni* and *P. pungens*), Douglas fir (*Pseudotsuga menziesii*), and quaking aspen (*Populus tremuloides*). Sample species at this site was Douglas fir. The other site is located in woodland on the northeastern slope of the plateau, 1.3 km south of Highway 89A on East Side Game Road. Abundant tree species are pinyon pine (*Pinus edulis*) and Utah juniper (*Juniperus osteosperma*). Big sagebrush (*Artemesia tridentata*) was the sample species at this site.

Growth ring techniques. Techniques of sampling, preparing, dating, and statistically interpreting growth rings of woody species are described elsewhere (Ferguson, 1964; Ferguson, 1970; Fritts, 1971; Fritts, 1976).

Douglas fir trees were cored using an increment borer. Big sagebrush plants were sectioned in the field. Douglas fir specimens were glued into grooved sticks after drying. Sagebrush specimens were reinforced with glue, since the discontinuous cambrium makes these specimens very fragile. Specimens were sanded to a smooth finish using progressively finer grades of sandpaper. Rings were crossdated, as described by Fritts (1976), and each dated ring was measured to the nearest 0.01 mm using a Banister's measuring machine.

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The width of a particular ring is a function of the individual plant's age-dependent growth rate, climatic factors, and local site factors: A standardization procedure, developed at the Laboratory of Tree Ring Research (LTRR) in Tucson, removes growth anomalies peculiar to individual plants (Fritts, 1976). Standardized ring width indices are observed ring widths divided by expected ring widths based on a fitted growth curve for each plant. Average ring width index for each radius (= core) is 1.0, and variance in ring width index is independent of tree age when a particular group of rings formed. Averaging index values for each year for all radii removes the effect of local site factors, and results in a master chronology for the site.

Hunting success as an index of deer numbers. Hunting success was used as an index of relative deer numbers because it is available for North Kaibab hunting seasons from 1924 to present (Table 1). Deer hunting success (percentage of hunters successfully harvesting a deer in a given year) should vary positively with deer numbers. This is a common assumption in wildlife studies (e.g. Dasmann and Dasmann, 1963; Smith and Gallizioli, 1965), but the relationship between deer numbers and hunting success is unknown on the North Kaibab. There was considerable variation in deer hunt structure during 1925-1975, making it difficult to evaluate the reliability of changes in hunting success as estimates of changes in deer numbers.

Climate - ring width relationships. Variation in ring width indices were related to variations in temperature and precipitation at Grand Canyon, Arizona (Sellers and Hill, 1974). The weather station is located across the Grand Canyon, about 33 km from the Douglas fir site and about 75 km from the sagebrush site. Elevation at the weather station is 2126 m; this is lower than the Douglas fir site (2745 m) and higher than the sagebrush site (2060 m). Comparably consistent and reliable data are not available on the North Rim of the Canyon for such a long period (1931 - present).

Table 1. Hunting success on the North Kaibab, 1925-1975. Hunting success is the ratio of hunters to animals killed, expressed as a percentage. (Russo, 1964; Arizona Game and Fish Department files)

YEAR	HUNTING SUCCESS	YEAR	HUNTING SUCCESS	YEAR	HUNTING SUCCESS
1925	98.0	1942	85.4	1959	55.3
1926	94.5	1943	75.5	1960	40.1
1927	88.6	1944	71.4	1961	31.3
1928	95.0	1945	56.5	1962	46.5
1929	155.0	1946	63.7	1963	54.7
1930	186.0	1947	70.8	1964	58.0
1931	89.7	1948	62.6	1965	38.1
1932	92.8	1949	54.4	1966	49.7
1933	91.3	1950	62.7	1967	22.0
1934	83.5	1951	53.0	1968	37.6
1935	84.8	1952	66.9	1969	43.9
1936	86.2	1953	84.5	1970	40.5
1937	71.1	1954	75.7	1971	48.5
1938	79.3	1955	55.9	1972	48.1
1939	64.6	1956	62.2	1973	51.7
1940	78.0	1957	60.2	1974	46.0
1941	67.0	1958	59.6	1975	44.6

Mean temperature and total precipitation for the following intervals were used in multiple regression to predict Douglas fir and sagebrush ring-width indices (after Fritts, 1965): (1) previous June; (2) previous July; (3) previous August - September; (4) previous October - November; (5) previous December, current January - February; (6) current March - May; (7) current June; and (8) current July. Additionally, ring width indices from the previous three years were included as predictors to allow for possible effects of prior growth.

Ring width - hunt success relationships. Any relationship between hunting success and ring width index will lag, perhaps by a number of years. The extent of the lag depends upon the nature of the effect. Direct effects, such as snowfall impeding deer movement and leading to starvation, act with little lag. Indirect effects, like the influence of climate on deer through quality of the range, will have longer lags. Primary effects, those felt by extant individuals, act with short lags. Secondary effects, effects on animals which could have lived at future times, may be associated with long time lags.

If these different kinds of effects are important, then ring widths should be related to deer numbers using a number of different lags. In this view, the deer population summarizes the effects of climate over a number of years. This is analogous to the way a single tree integrates effects of climate over current and previous growing seasons in producing an annual ring.

Spearman's rho statistic (Conover, 1971) was calculated for the correlation between hunting success and ring width index, using lags of 0-19 years in the growth rings. Unadjusted multiple tests present difficulties because of the uncertainty of the level of significance. Significances of correlations were adjusted to more conservative levels (after Cooper, 1968).

To determine how accurately hunting success is predicted using tree rings, several multiple regressions were performed. Using the Douglas fir chronology, stepwise regressions were performed including and excluding previous hunting success as a predictor. For each of these cases, lags in the tree rings of 0-9 years, 6-15 years, and 10-19 years were included. The log transformation (Bartlett, 1947) was applied to the hunting success data.

RESULTS. - *Chronologies.* Tables 2 and 3 present the master chronologies for the Douglas fir and sagebrush sites, respectively. The final Douglas fir chronology includes 42 radii; the sagebrush chronology includes 38 radii. The Douglas fir chronology has a serial correlation coefficient (r) of 0.67, and includes 283 years of data (1693-1975). The big sagebrush chronology (serial $r = 0.06$) includes 71 years of data (1905-1975). Mean sensitivity, a statistic developed at the LTRR, measures the degree to which an index value is different from its predecessor (Fritts, 1976). Greater mean sensitivity indicates greater year to year variability in ring width indices. Mean sensitivity for the Douglas fir chronology is 0.17; mean sensitivity for the sagebrush chronology is 0.27.

Climate - ring width relationships. Climate - ring width regressions for both sites are significant ($p < 0.001$) (Table 4).

Douglas fir responded positively to prior growth, precipitation in previous July, precipitation in current March through July, and temperature in previous July. Temperature in previous August - September was negatively related to ring width index in Douglas fir. Sagebrush did not respond significantly to prior growth. Growth in sagebrush was positively related to precipitation in previous October - December, precipitation in current January - February, and temperature in previous July. Sagebrush growth was negatively related to precipitation in previous August - September and current June, and temperature in current March - May. These two species responded differently to climate and prior growth.

Ring width - hunting success relationships. There were no significant ($p \leq 0.05$) correlations between sagebrush ring width indices and hunting success (Table 5). Sagebrush growth rings were not useful in predicting hunting success on the North Kaibab.

All time lags tested using the Douglas fir data were significant ($0.01 < p < 0.05$) (Table 5). All correlations were positive.

Table 6 presents the multiple regression equations obtained. All six equations are significant ($n = 51$, $p < 0.05$); five of the six are highly significant ($p < 0.001$). In one case (short lag, previous hunting success excluded) residuals are not independent (Run's Test, $p \leq 0.05$). All relationships are positive. Similar results were obtained, with smaller

Table 2. The Douglas fir chronology.

YEAR DECADE	0	1	2	3	4	5	6	7	8	9
1693				0.79	1.04	0.94	1.36	1.19	1.68	2.13
1700	0.22	0.24	0.76	0.67	0.99	0.89	0.72	0.76	0.66	0.74
1710	0.90	0.63	0.57	0.75	0.70	0.71	0.78	1.06	0.99	0.90
1720	0.96	1.03	0.75	0.63	1.09	1.15	1.08	0.89	0.79	0.66
1730	0.69	0.90	0.89	0.77	0.71	0.64	1.18	0.84	0.97	0.81
1740	0.80	1.33	0.95	1.30	0.99	1.08	1.25	1.14	0.81	1.11
1750	0.71	0.84	0.90	1.06	1.10	1.00	1.21	1.64	1.38	1.28
1760	1.02	1.10	1.08	0.86	1.29	1.19	1.16	1.39	1.08	1.19
1770	1.36	1.34	1.00	0.79	0.98	1.01	1.03	1.09	1.01	1.46
1780	1.04	1.23	1.10	1.66	1.87	1.34	1.17	1.67	1.06	1.01
1790	1.14	1.08	1.10	1.10	1.43	1.22	1.12	0.92	0.97	1.02
1800	0.87	0.64	0.94	0.74	0.85	0.71	0.79	0.82	0.88	0.91
1810	0.92	0.97	0.86	0.69	0.90	0.87	0.97	0.87	0.76	0.77
1820	0.70	0.92	0.67	0.89	0.88	0.79	0.87	0.97	1.17	0.91
1830	0.77	0.90	0.64	0.52	0.47	0.55	0.38	0.51	0.54	0.73
1840	0.64	0.54	0.48	0.59	0.60	0.41	0.52	0.43	0.62	0.93
1850	0.85	0.69	0.69	0.71	0.66	0.72	0.61	0.73	0.76	0.62
1860	0.62	0.52	0.81	0.58	0.44	0.59	0.76	0.89	1.08	1.08
1870	1.12	1.02	1.00	0.90	0.94	0.81	0.76	0.90	0.85	0.52
1880	0.63	0.82	0.79	0.93	1.09	1.15	1.05	1.21	1.18	1.14
1890	1.19	1.13	0.97	0.77	0.94	1.03	0.81	1.09	1.10	0.69
1900	0.91	1.04	0.85	1.16	0.93	1.07	1.42	1.31	1.52	1.66
1910	1.33	1.73	1.40	1.35	1.54	1.37	1.43	1.43	1.08	1.32
1920	1.21	1.35	1.23	1.42	1.19	1.29	1.26	1.36	1.16	1.15
1930	1.25	1.21	1.11	1.07	1.17	1.32	1.10	1.40	1.21	1.08
1940	1.05	1.24	1.10	0.99	1.03	0.83	0.78	0.91	0.86	0.79
1950	0.70	0.64	0.87	0.88	0.89	0.93	0.72	0.86	0.87	0.81
1960	0.77	0.72	0.87	0.68	0.87	0.99	0.96	0.92	1.17	1.26
1970	1.01	1.01	1.08	1.23	0.83	1.50				

sample size, using Stockton's Kaibab chronology obtained from Douglas fir (no. 190300, Drew, 1972).

DISCUSSION. — These results suggest that, in the long term, Douglas fir trees and deer numbers are responding in similar ways to changes in climatic suitability.

Weather data are less useful in predicting sagebrush growth, as compared to Douglas fir growth (Table 4). The difference in explained variance has at least three possible explanations. First, big sagebrush responded less strongly to prior growth than did Douglas fir. Second, perhaps big sagebrush responds less strongly to these particular climatic variables than does Douglas fir. Either a redefinition of the climatic variables is implied, or other factors (herbivory?) more often limit sagebrush growth. Third, the difference may simply be a function of greater distance of the sagebrush site from the weather station (less climatic similarity).

Additional evidence is obtained by comparing hunting success - ring width index relationships for the two species. Douglas fir growth is a good predictor of future hunting success, sagebrush growth is not. Ring widths of plants that escape browsing are expected to correlate positively with deer numbers. Climatic conditions favoring increased growth of trees also favor increases in deer numbers. Ring widths of plants which are periodically damaged by browsing (like big sagebrush) are expected to show little or no correlation with deer numbers (Table 5). Perhaps large numbers of browsing deer suppress growth in these plants, regardless of climatic conditions. When deer numbers are low, the plants again respond to climate. Ring widths of preferred browse species, such as cliffrose (*Cowania mexicana*) are expected to correlate negatively with deer numbers, although the relationship will be weak. Climate may be unfavorable when deer numbers are low, producing limited growth even though the plants

Table 3. The big sagebrush chronology.

YEAR DECADE	0	1	2	3	4	5	6	7	8	9
1905						1.38	1.16	1.87	1.35	1.11
1910	0.92	1.02	0.92	0.84	1.17	0.99	1.08	1.17	0.77	0.93
1920	1.13	0.53	0.95	0.89	0.88	0.84	1.14	1.03	1.07	0.76
1930	0.70	0.67	1.55	1.28	0.84	1.35	0.77	1.13	1.08	0.91
1940	0.92	1.08	1.04	1.13	1.10	0.91	0.77	0.90	1.36	1.23
1950	1.07	0.46	1.27	0.85	0.89	0.62	0.71	1.36	1.20	0.61
1960	1.34	0.97	1.00	1.10	1.01	1.52	1.24	0.95	1.11	0.95
1970	0.65	0.72	0.64	1.25	0.81	1.41				

Table 4. The relationship between ring width indices and climate and prior growth on the Kaibab plateau, 1932-1972.

	SIGNIFICANT PREDICTORS				
SITE	PRECIPITATION	TEMPERATURE	PRIOR GROWTH	R^2	REGRESSION SIGNIFICANCE
DOUGLAS FIR	PREVIOUS JULY CURRENT MARCH-JULY	PREVIOUS JULY-SEPTEMBER	FIRST YEAR THIRD YEAR	0.83	$p < 0.001$
BIG SAGEBRUSH	PREVIOUS AUGUST-DECEMBER CURRENT JUNE	PREVIOUS JULY CURRENT MARCH-MAY	NONE	0.57	$p < 0.001$

Table 5. Spearman's rank correlation coefficients for correlation between Kaibab deer hunting success and ring width indices of big sagebrush and Douglas fir in current and previous years. Period covered by the analysis is 1925-1975. See text for significance levels.

TIME LAG (YEARS)	HUNTING SUCCESS CORRELATION WITH: BIG SAGEBRUSH	DOUGLAS FIR
0	-0.045	0.441
1	-0.053	0.514
2	-0.163	0.499
3	-0.096	0.568
4	-0.107	0.615
5	-0.064	0.672
6	-0.098	0.673
7	-0.237	0.670
8	-0.205	0.685
9	-0.078	0.784
10	-0.060	0.768
11	-0.062	0.804
12	-0.097	0.797
13	-0.115	0.793
14	0.034	0.759
15	0.074	0.848
16	0.084	0.867
17	-0.072	0.874
18	0.042	0.790
19	0.124	0.836

are released from browsing. To my knowledge, cliffrose has not been examined in growth ring studies.

Previous hunting success is as good a single predictor of hunting success as any of the lags in the tree rings. First-order Spearman's autocorrelation coefficient for the hunting success data is 0.88.

The tree ring record may be useful in evaluating deer numbers during, for example, prehistoric periods. The general process is to construct a regression equation for the period when deer data are available, then use the equation to reconstruct past numbers (Fritts, 1976; Stockton and Fritts, 1973).

Of course, there is danger in such extrapolation. The basic assumption is that the relationships between variables are the same during the calibration and prediction periods. For animal populations inhabiting areas under human influence, this is not likely to be true in modern times. The relationship between deer hunting success and ring width indices might have been much different, for example, if wolf and mountain lion populations on the Kaibab were not controlled. From this view, Rasmussen (1941) may have been correct in partially attributing the 1900-1924 deer increase to predator control, although the present study suggests the increase was augmented by a period of favorable climatic conditions.

The three regression equations excluding previous hunting success (Table 6) provide perfectly ambiguous predictions of hunting success through the late 1970's, compared to the early 1970's. Average hunting success for 1970-1975 was 46.6%. The short lag (0-9 yr) equation predicts average hunting success for 1976-1979 at 71.1%; the intermediate lag (6-15 yr) equation predicts 48.2% and the long lag (10-19 yr) equation predicts 39.0%. Observed hunting success in 1976 was 49.1%. In 1977 and 1978, with a bucks-only hunt

Table 6. Multiple regression of Kaibab deer hunting success on previous hunting success and Douglas fir ring width indices, 1925-1975. H_0 = current hunting success, H_1 = previous hunting success, F_i = ring width index lagged i years.

	LAG (YR)	EQUATION	R^2	P
H_1 IN	0-9	$Log(H_0) = 0.6670 + 0.0027 F_9 + 0.4711 Log(H_1)$	0.66	< 0.001
	6-15	$Log(H_0) = 0.7766 + 0.014 F_6 + 0.0030 F_{15} + 0.3020 Log(H_1)$	0.73	< 0.001
	10-19	$Log(H_0) + 0.9041 + 0.0018 F_{15} + 0.0017 F_{16} + 0.0014 F_{19} + 0.1908 Log(H_1)$	0.75	< 0.001
H_1 OUT	0-9	$Log(H_0) = 1.1749 + 0.0021 F_4 + 0.0040 F_9$	0.55	< 0.05
	6-15	$Log(H_0) = 1.1089 + 0.0023 F_6 + 0.0041 F_{15}$	0.68	< 0.001
	10-19	$Log(H_0) = 1.1173 + 0.0019 F_{15} + 0.0024 F_{16} + 0.0017 F_{19}$	0.74	< 0.001

structure, success dropped to 21.8% and 26.9%, respectively (Russo, 1979, pers. comm.). Presumably, the bucks-only structure reflects a drop in deer numbers. The long lag equation predicts a drop, and it is the best equation in terms of explained variation (R^2) (Table 6). The same equation predicts a general upturn in success through the 1980's.

SUMMARY. — Measuring the long-term effects of biotic and abiotic factors on natural populations is difficult. Comparison between Douglas fir ring width indices and Kaibab deer hunting success suggests that regional climatic variation affects the long range capacity of the area to support deer. A long term perspective on populations may prove useful in documenting unsuspected causes of fluctuations. Leopold et al. (1947) estimated that about 100 deer herds in the United States entered an irruptive oscillation between 1900 and 1945. An interesting research problem, with possibly significant management implications, is the consideration of these oscillations in light of tree ring records.

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